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Fishery Production Potential on the Northeast Continental Shelf of the United States

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Introduction

Attempts to define the fishery production potential of marine systems based on patterns of energy flow have an extensive history (Kestevan and Holt, 1955; Graham and Edwards 1962; Schaefer 1965, Ricker 1969; Ryther 1969; Gulland 1970). Bottom-up control of fish production has now been demonstrated in many regions of the world ocean (Ware 2000), supporting the general approach of tracing pathways involved in the translation of primary production to fishery yields. Estimates of accessible global fish production potential derived in this way vary but are on the order of one hundred million tons although the convergence of these estimates may largely reflect shared assumptions and countervailing errors (Pauly (1996). The yield of marine capture fisheries is now approaching this level (FAO 2006).

The Northeast Continental Shelf of the United States has supported important commercial fisheries for several centuries (Murawski et al. 1997). Investigations into the determinants of fishery production potential of this region were initiated with the seminal studies of Clarke (1946) on Georges Bank. Energy budgets for this system have since been progressively expanded and refined (Cohen et al. 1982; Sissenwine et al. 1984; Steele et al. 2007; Link et al. 2006).

Estimation of fishery production potential on the Northeast Continental Shelf based on determination of standing stock biomass and specification of a system-wide exploitation rate has been explored in several studies. Edwards (1968) provided an estimate of total fish biomass on the northeast shelf and suggested that a yield of 1.80-2.26 million tons could be extracted by “a highly organized, versatile, and efficient fishery paying due attention to the principles of good fishery management”. Hennemuth (1976) estimated that fish yield in this region could potentially reach 1.3 million tons (cited in Cohen et al. 1982). Gulland (1970) subsequently provided an estimate of fishery production potential on the U.S. Northeast Continental Shelf of 1.55 million tons based on extrapolation of observed production levels.

Aggregate surplus production models for this system have also been applied to estimate the maximum sustainable yield of exploited fishfish populations (see Overholtz et al. 2008). Au (1973) developed an aggregate surplus production model for finfish on the Northeast Continental Shelf for the period 1961-71 and provided an estimate of maximum sustainable yield of 0.95 million tons. Brown et al. (1976) subsequently updated the aggregate production model estimates for this region and reported a system-wide estimate of MSY of 0.9 million tons of finfish. This estimate was contrasted with the sum of individual-species MSY estimates (1.3 million tons) and it was inferred that species interactions accounted for the discrepancy between the aggregate and individual-species estimates.

Au (1973) provided an alternative estimate of fishery production potential of 1.5-3.8 million tons based on energy flow estimates for the Northeast continental shelf. The reported range principally reflects different assumptions concerning the mean trophic level of the catch in this analysis. Here, we revisit the issue of estimation of potential fishery yield on the Northeast Continental Shelf based on primary production and energy transfer through successive trophic levels. We explicitly consider production and potential yield of both nektonic species and macrobenthic invertebrates supporting commercial fisheries. We further note the importance of accounting for consumptive demand of marine mammals, sea birds, sea turtles in the assessing potential yield from the system.

Methods and Data Sources

The fishery production potential (P_f) for a region is a function of the amount of primary production elaborated, the fraction of this production available to higher trophic levels, the transfer efficiency between successive trophic levels, and the number of trophic levels through which energy must be transferred. The production potential can be expressed:

$$P_f = R \cdot PP \prod_{i=1}^{n} \tau_i$$

where R is the fraction of photosynthetic products retained within the system (accounting for advective loss and/or burial in sediments), PP is the primary production, and τ_ι is the transfer efficiency between successive trophic levels (TL) and n is the number of trophic levels. In practice, because of the mixed trophic level composition of the diet of most marine predators, fractional trophic levels are assigned to each predator. We assumed a retention rate of 0.9 to reflect some advective loss from the continental shelf margin as a result of entrainment by rings and eddies. Direct estimates of burial in sediments were not available and no allowance is made for this factor. We therefore consider our retention value to reflect a minimum loss estimate. In our analysis, we recognize two pathways for transfer of primary production in the system -- the classical grazing food chain tracing the fate of new primary production, principally by diatoms, and production involving transfer through the microbial food web originating with nanoplankton production . The former involves grazing by mesozooplankton and filtering of diatom production by benthic invertebrates, particularly bivalves. The latter pathway entails consumption of nanoplankton by heterotrophic bacteria and feeding of microzooplankton on bacteria. Carnivorous zooplankton prey on microzooplankton in this representation. The microbial pathway therefore involves two or more trophic transfer steps before reaching mesozooplankton as a bridge to higher trophic levels

Primary Production

We employed satellite-derived estimates of primary production for the region using a modification of the Vertically Generalized Productivity Model (VGPM, Behrenfeld and Falkowski 1997) as specified by (O'Reilly and Ducas 2004). O'Reilly and Ducas (2004) demonstrated that this algorithm (designated VGPM2) provided the best agreement with *in situ* observations of the seasonal productivity cycle for the Northeast shelf ecosystem. Link et al. (2006) employed these results in an analysis of energy flow on the Northeast Continental Shelf. The VGPM2 algorithm provided a shelfwide estimate of primary production of 364 gC $m^{-1}yr^{-1}$ for observations averaged over the period 1997-2002. We used estimates of the proportion of primary production attributable to net phytoplankton and to nanoplankton based on information provided by O'Reilly et al. (1987) and O'Reilly and Zetlin (1998) to partition the different energy pathways included in the model.

Transfer Efficiencies

Estimates of transfer efficiencies between successive trophic levels were based on information in the literature for the microbial food web and on direct estimates from network models derived for this system (Link et al. 2006). For the microbial food web, we assumed that 50% of the nanoplankton is consumed by heterotrophic bacteria (Ware 2000). The gross growth efficiency of bacteria was taken to be 33% and the assimilation fraction to be 80% (Link et al. 2006). The transfer efficiency from bacteria to microzooplankton was taken to be 0.25 (Ware 2000).

For the grazing food chain, we partitioned the system into transfer from net phytoplankton to mesozooplankton and macrobenthic invertebrates and transfer from mesozooplankton to higher trophic levels. An emerging generalization is that the transfer efficiency from the first to second trophic level for this component is approximately 20% while the transfer efficiency between successive higher trophic levels is on the order of 10-15% (e.g. Lalli and Parsons 1997). For our data, the estimated transfer from net phytoplankton to secondary producers is 18.8 % and for all higher trophic levels it is 13.2% based on Ecopath results. These estimates are based on a weighted average of results from network models for four subregions of the Northeast Continental Shelf. We compared our results with similar estimates for North American temperate and boreal marine systems (Table 1). The higher latitude systems are characterized by generally lower transfer efficiencies. The highest estimates were for the Gulf of Alaska and for the Northeast Shelf. The mean transfer efficiency from the first to second trophic level was 0.164 (SD=0.048) and between successive higher trophic levels it was 0.106 (SD=0.031).

Estimated fishery production potential using this general approach is known to be particularly sensitive to the transfer efficiencies employed (e.g. Au 1973; Miller 2004). We therefore explored the consequences of uncertainty in transfer efficiencies based on the observed range in the North American studies cited above. Monte Carlo simulations were conducted with transfer efficiencies between the first and second trophic levels and between successive higher trophic levels drawn from Beta distributions with mean and variances specified by the unweighted averages of the North American studies. Parameters of the Beta Distribution were determined by the iterative method suggested by (Johnson et al. 1995).

Catch Data

We employed catch data (live weight) as reported to the North Atlantic Fisheries Organization for the Northeast Continental Shelf (NAFO Statistical Areas 5 and 6). Catch data for all species in this region was extracted and examined for principal distribution areas. To maintain a focus on the continental shelf system and to separate species relying on different nearshore energy pathways, we removed species found principally in estuarine and immediate coastal environments from further consideration. These included nearshore bivalve and crustacean species, all anadromous species, and Atlantic menhaden. Peter and Schaaf (1990) note a strong dependence on detrital pathways in production of estuarine and immediate coastal areas and for this reason, we did not consider species with a strong estuarine dependence.

Wigley et al. (2008) provide estimates of discards in the commercial fishery in 2005 for thirty-three species. We used these estimates (adjusted for survival of discarded fish; Table 5a of Wigley et al. 2008) to provide a more complete accounting of removals from the system in 2005. Similarly, we extracted 2005 recreational catch estimates from the MRFSS data base (http://www.st.nmfs.noaa.gov/st1/recreational) for the Northeast Continental Shelf to make a more detailed assessment of removals and sources of extraction in that year. Discard estimates from the recreational fishery were extracted and we applied a mortality rate of 15% to all species released alive.

To track changes in the trophic structure of the catch and its implications for patterns of energy utilization, we computed the mean trophic level of species in the catch (weighted by the proportional representation of each species). We assigned a trophic level (TL) to each species using designations in the compilation provided by FishBase (http://www.fishbase.org). These characterizations largely reflect the trophic level of adult individuals and do not capture the ontogentic shifts in diet characteristic of most marine species.

Based on the foregoing, we can estimate the primary production required (*PPR*) to support observed fishery production as:

$$PPR = R^{-1} \cdot C_c \prod_{i=1}^{n} \tau^{-1}$$

Where C_c is the total catch (expressed in carbon units) (see also Pauly and Christensen 1995). We translated from carbon to wet weight using a factor of 7.9 (Vinogradov 1973). Note that because a full time series of primary production estimates are not available, we applied the mean for the period 1997-2002 (Link et al. 2006) thoughout this analysis. To the extent that primary production levels may have changed over this period, the estimates of PPR would have to be adjusted.

MSY Estimates

We augmented the compilation of MSY estimates provided by Overholtz et al. (2007; Table 5) to include invertebrate species and individual species represented in the demersal omnivore, demersal piscivores, demersal benthivores, and medium pelagics categories (Table 7 of Overholtz et al. 2007) of all species for which reference points were available. MSY estimates for goosefish, ocean pout, tilefish, bluefish, Atlantic croaker, striped bass, and shortfin squid were obtained from Status of the Fishery Resources of the Northeastern United States (http://www.nefsc.noaa.gov/sos/index.html) and/or consultation with assessment scientists responsible for these species.

The MSY estimates for the dominant bivalve species (Surf Clams, Ocean Quahogs, Sea Scallops) are expressed in terms of meat weight. Because we are ultimately interested in providing an energy flow context for ecosystem harvesting strategies, we included the carbon content of shell material (~10% of total shell weight; Vinogradov 1953) in a revised MSY estimate. For scallops, MSY is expressed in terms of adductor muscle weight. We further accounted for scallop visceral mass in our estimates.

To explore the consequences of harvesting all species at their MSY levels, we computed the mean trophic level of the catch that would result under an MSY harvest policy and used these estimates to determine the predicted level of overall production predicted.

Consumptive Demand for Protected and Endangered Species

An emerging concern in marine ecosystem-based management is ensuring that the energy demands of protected resource species is considered in establishing harvesting strategies for a region. We employed estimates of the consumption to biomass ratios for marine mammals, sea turtles, and sea birds in concert with biomass estimates to generate estimates of total consumption based on EMAX estimates (Link et al. 2006). Ideally, we would incorporate biomass estimates corresponding to target population levels for these species in assessing overall energy demands in the system. Unfortunately explicit designation of optimum population levels have not been made and we have therefore used the current biomass as defined in EMAX analyses with the recognition that these represent an underestimate of the required energy levels for rebuilt populations. We made similar estimates for large shark and other apex predator species using this approach to reflect requirements at the highest trophic levels.

Results

The total yield of the for the Northeast Continental Shelf for the period 1961-2005 has remained relatively stable over the last three decades after an initial perturbation due to the arrival of distant water fleets in this region (Figure 1). The distant water fleet targeted underutilized species (principally small pelagic fishes as well as traditionally harvested species (e.g. gadoid and flatfish species). Despite the relative stability of the catches following the perturbation induced by distant water fleet activities, the contribution of different taxonomic groups has changed markedly with a current dominance by small pelagic fishes and bivalves (in terms of live weight landed). Escalating targeted fishing on traditional groundfish species during the first decade of the distant water fleet activities resulted in sharp declines in this component (Figure 1), notably for haddock. Sequential declines then followed for several groundfish species, most notably silver hake, High initial catches of small pelagic fishes by the distant water fleet were not ultimately sustainable and declined to lower but proportionally significant components of the catch. The economic importance of bivalve fisheries has progressively increased and is reflected in the catch history in the region.

The depletion of the traditionally harvested groundfish species resulted in an overall initial decline in the mean trophic level of the catch (Figure 2). During the period 1960-70, the mean trophic level averaged 3.28 but subsequently declined to 2.74 in 2005, reflecting the compositional changes noted above. Calculations of the primary production required to account for the observed catch indicate a rapid increase to high levels, approaching 35 % during the first decade of exploitation by the distant water fleet (Figure 3). The transition to a fishery dominated by lower trophic level species is reflected in the sharp decline and subsequent stabilization at a much lower level of appropriation of available primary production. The estimate of the primary production required to support the commercial fishery alone in 2005 was 7.2%. When discard estimates and recreational catch is added, the estimate for required primary production is 9.55%.

Under an MSY harvest policy, the estimated mean trophic level for all species for which MSY reference points are currently available would be approximately 3.1. We consider this to be a minimum estimate because reference points for a number of high level predators are not currently available and therefore not incorporated. Mean trophic level exceeded this benchmark during the period of distant water fleet activity. We explored predicted production levels over a range of mean trophic levels of 3.0 to 3.25 to encompass a probable span of trophic levels under an MSY harvest policy. Our estimate of system-wide production under this range is 4.8-6.2 million mt.

We are ultimately interested in translating production to estimates of sustainable catch from the system (representing commercial and recreational landings and discards). Quantitative guidelines for ecosystem exploitation rates have not yet been established. We explored possible exploitation levels ranging from 0.25 to 0.35 judged to be reasonable for an ecosystem exploitation rate (e.g. Miller 2005; Figure 4). For a mean trophic level of the catch of 3.1 and an ecosystem exploitation rate of 0.3, the predicted catch level (landings plus discards) from the system as a whole is 1.855 million tons (fish and invertebrates). For a mean trophic level of the catch of 3.2 and an ecosystem exploitation rate of 0.3, the predicted equilibrium catch level is 1.55 million tons. The sum of the MSY levels for the GARM species, pelagics (herring, mackerel, and butterfish), and small elasmobranchs (dogfish and skates) is 0.569 million tons (Overholtz et al 2008). The estimated bivalve (surf clam, ocean quahog, and sea scallop) MSY level (accounting for body mass and 10% of the shell mass) is 0.535 million tons. The MSY accounted for by combining all of these estimates components is 1.29 million tons. There is a substantial unrepresented component of biomass and potential yield not reflected in MSY estimates available in the partial accounting of system structure identified above. If we take a mean trophic level of the catch of 3.2 and a 30% exploitation rate, then the MSY levels in the partial accounting above comprise 83% of the estimated production potential. Alternatively, if we accept a mean trophic level of the catch of 3.1 at MSY and a 30% ecosystem exploitation rate, approximately 70% of the available production is taken up. These estimates do not include allowance for landings of species not included in partial accounting above. Nor do they include discard levels for all species. This suggests that the available demand will be exceeded in both cases when these considerations are taken into account.

Uncertainty in Transfer Efficiencies

Estimates of the fishery production potential using the mean transfer efficiencies and their standard deviations for North American studies results in a coefficient of variation of 55.1%. The mean fishery production potential was 4.02 million tons with 80% confidence intervals of 1.66-6.97 million tons. The probability distribution of production potential estimates for 10,000 iterations is provided in Figure 5. Because the estimates employed in this analysis are drawn from widely different systems, from temperate to boreal and subarctic conditions, we expect that the results encompass a greater range of variability than if more closely matched systems were available for use.

Ecosystem Overfishing

Although criteria for defining overfishing at an ecosystem level are only now emerging, approaches based on ecosystem indicator reference points have received increasing attention (e.g. Link 2005). Tudela et al. (2005) and Libralato et al. (2008) have constructed indices of ecosystem overfishing incorporating information on the primary production appropriated by fisheries and the mean trophic level of the catch. These indices were based on classification systems using independently assigned ecosystem status levels (overfished, sustainably fished) using the criteria of Murawski (2000) in conjunction with PPR and mean trophic level. Murawski (2000) suggested that an ecosystem could be considered overfished if one or more of the following critera were met:

- Biomasses of one or more important species assemblages or components fall below minimum biologically acceptable limits, such that:
  1) recruitment prospects are significantly impaired,
  (2) rebuilding times to levels allowing catches near MSY are extended,

(3) prospects for recovery are jeopardized because of species interactions,
(4) any species is threatened with local or biological extinction;

- Diversity of communities or populations declines significantly as a result of sequential ‘‘fishing-down’’ of stocks, selective harvesting of ecosystem components, or other factors associated with harvest rates or species selection;

- The pattern of species selection and harvest rates leads to greater year-to-year variation in populations or catches than would result from lower cumulative harvest rates;

- Changes in species composition or population demographics as a result of fishing significantly decrease the resilience or resistance of the ecosystem to perturbations arising from non-biological factors;

- The pattern of harvest rates among interacting species results in lower cumulative net economic or social benefits than would result from a less intense overall fishing pattern or alternative species selection;

- Harvests of prey species or direct mortalities resulting from fishing operations impair the long-term viability of ecologically important, non-resource species (e.g., marine mammals, turtles, seabirds).

Tudela et al. (2005) provided a meta-analysis of 49 ecosystems to which these criteria could be applied and for which estimates of PPR and mean trophic level were available. Multivariate analyses were used to define a demarcation point between overfished and sustainably fished systems in the PPR-TL plane (Figure 6). In this representation, losses incurred by fishing at low trophic levels affect the energy available to higher trophic levels (see also Libralato 2008) and the interplay between the primary production appropriated for fishery yield and the mean TL determines the ecosystem classification. Classification of ecosystem status for the Northeast Continental Shelf for several key points in the available time series are superimposed on the Tudela et al. (2005) phase plane. At the start of our series (1960), the system is classified as sustainably fished at the ecosystem level. At the height of distant water fleet activities, characterized by both high mean trophic level of the catch and high appropriation of available primary production. In the peak PPR year (1972) the highest index of ecosystem overexploitation was recorded (Figure 6). Despite the drop in PPR over the last two decades, the concomitant drop in mean trophic level results in an overfished classification in 2005 (Figure 6)

Conclusions

The estimates of production and potential yield from the Northeast Continental Shelf system are generally in accord with previous estimates for this region based on standing stock biomass estimates, aggregate surplus production, and energy flow considerations. Application of the first two methods for this region focused on fish populations and did not include economically important benthic invertebrate populations. In general, these earlier estimates also explicitly or implicitly considered that half the available biomass could be removed as catch. Au (1973) made the first projections of potential yield for the U.S. Northeast Continental Shelf based on energy transfer estimates. Au (1973) considered mean trophic level ranging from 2.5-3.0 for the catch and an assumed level of primary production of 250 gC $m^{-1}yr^{-1}$. Trophic transfer efficiency was assumed to be 0.10 from primary to secondary producers and 0.15 from secondary to higher level production units. Au further assumed that 70% of the available production could be taken as catch. Our estimates are consistent with the lower range of the projections made by Au but not the upper range. We attribute this discrepancy both to the very high exploitation rate considered feasible by Au and other underlying considerations of trophic transfer efficiencies and the amount of primary production actually available to support production at higher trophic levels.

We note that allowance for rebuilding of threatened and endangered species and of overexploited upper level predators must also be made in considering the overall system constraints on harvesting. Consideration of the estimated consumptive demand of major species groups including marine mammals sea turtles, sea birds, and highly migratory provides an overall context for the potential implications of rebuilding strategies on system energetics. The estimated overall consumption of these major species groups derived from EMAX estimates for average biomass levels during 1996-2000 is 2.57 million tons (Table 2) which substantially exceeded the harvest during this same time period. While consumption is included implicitly in the energy flow calculations, the tradeoffs between harvesting and the energetic demands of other predators must be considered.

Under our best current estimates of trophic structure and processes of the Northeast Continental Shelf, the amount of primary production available and consideration of total removals from the system at MSY levels, and future needs for threatened species and apex predators under rebuilding strategies, it appears that important constraints on the available energy must be considered in setting harvest policies. This perspective of course includes consideration of a much broader representation of the Northeast Shelf system than just the groundfish species under consideration in the GARM and tradeoffs among harvesting of GARM species and other system components. The metrics developed by Tudela et al. (2005) and Libralato et al. highlight the tradeoffs of harvesting at lower trophic levels and the condition of other ecosystem components. If changes in system productivity states resulting in lower growth rates for groups of species (see O'Brien et al. 2008) are confirmed, the ecological transfer efficiencies for these components will shift to lower levels and the estimated fishery production potential will be correspondingly lower.

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Table 1. Estimates of ecological efficiencies for North American marine ecosystems for transfer between trophic levels I-II and between II-II+ for the grazing food chain.

Region	TE (I-II)	TE(II-II+)	Source
Labrador-Newfoundland 1985-87	0.155	0.116	A. Bundy, Pers. Comm.
Labrador-Newfoundland 1995-2000	0.112	0.0747	A. Bundy, Pers. Comm.
Eastern Scotian Shelf 1980-85	0.081	0.115	A. Bundy, Pers. Comm.
Eastern Scotian Shelf 1990-95	0.15	0.088	A. Bundy, Pers. Comm.
Georges Bank	0.1704	0.10821	EMAX
Southern New England	0.2038	0.1358	EMAX
Mid_Atlantic	0.1922	0.10755	EMAX
Gulf of Maine	0.18277	0.17046	EMAX
Bering Sea	0.14395	0.0646	K. Ayden, Pers. Comm.
GOA	0.2538	0.0847	K. Ayden, Pers. Comm.

Table 2. Estimates of consumptive demand for threatened and endangered species, and apex predators.

Species Group	Consumptive Demand (mt)
Sharks- coastal	9517.873
Sharks- pelagics	9757.914
Highly Migratory Species	109224.6
Baleen Whales	1429008
Odontocetes	934722.3
Sea Birds	74002
Total	2566233

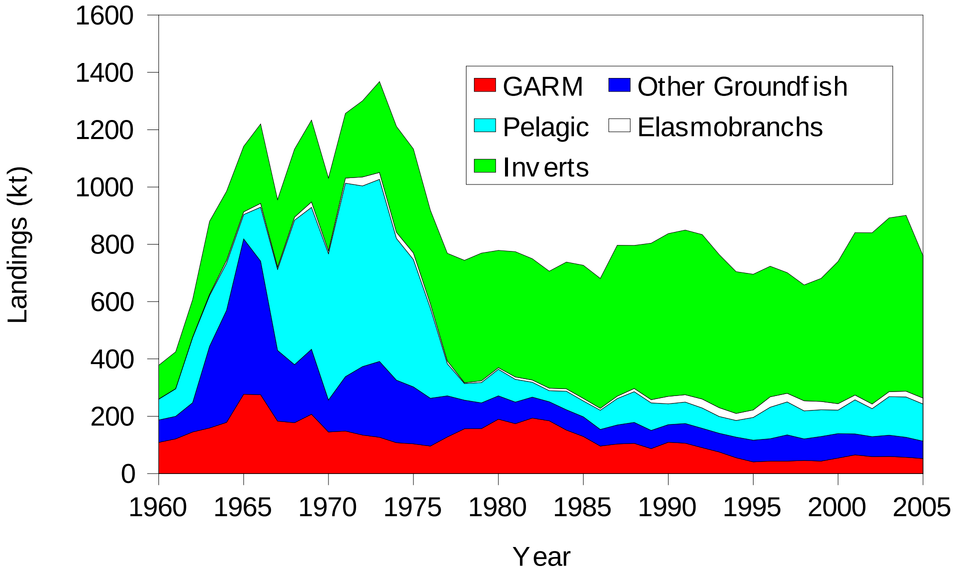

Figure 1. Reported landings (kt live weight) for the Northeast Continental Shelf (NAFO Areas 5 and 6) by species group.

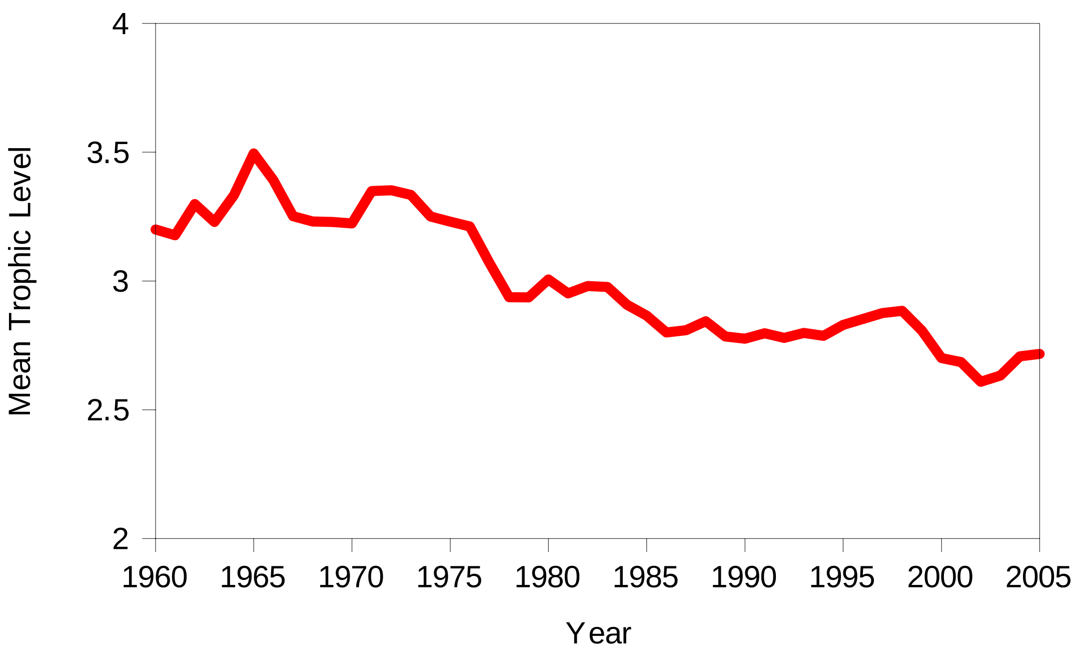

Figure 2. Trends in mean trophic level of the catch for the Northeast Continental shelf 1960-2005.

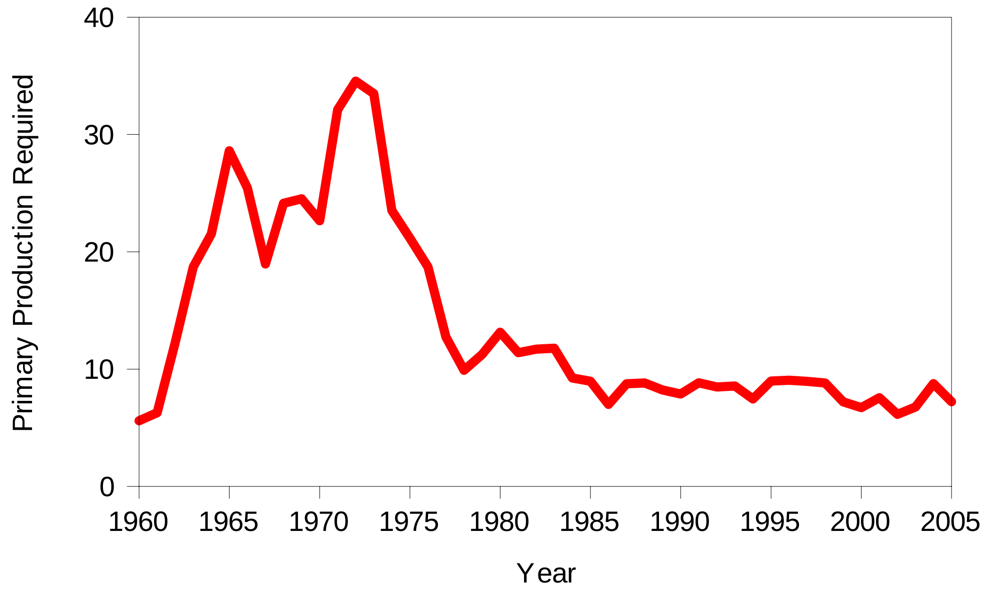

Figure 3. Trends in Primary Production Required (PPR) for observed catch and mean trophic level for the Northeast Continental Shelf (1960-2005)

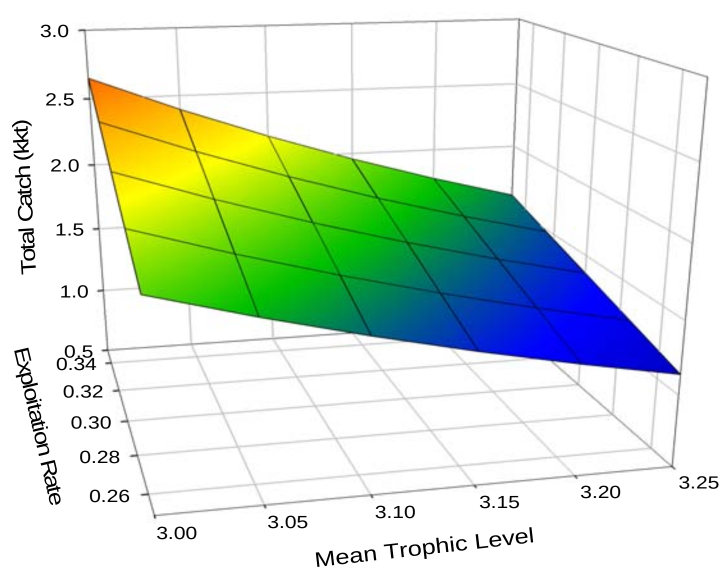

Figure 4. Estimated yield as function of the mean trophic level of the catch and the ecosystem exploitation rate

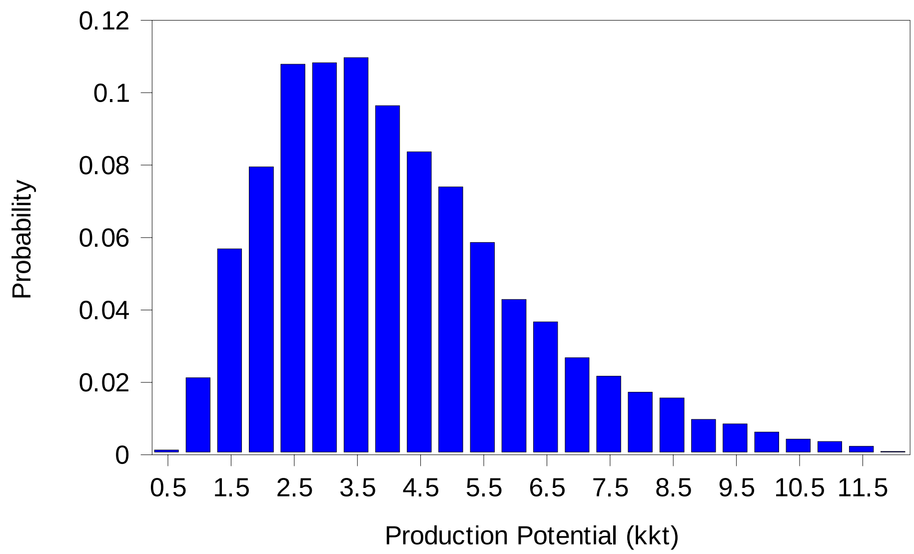

Figure 5. Probability distribution of estimated production potential for the Northeast Shelf under the assumption that transfer efficiencies are drawn from Beta distributions with means and variances specified from observed North American systems.

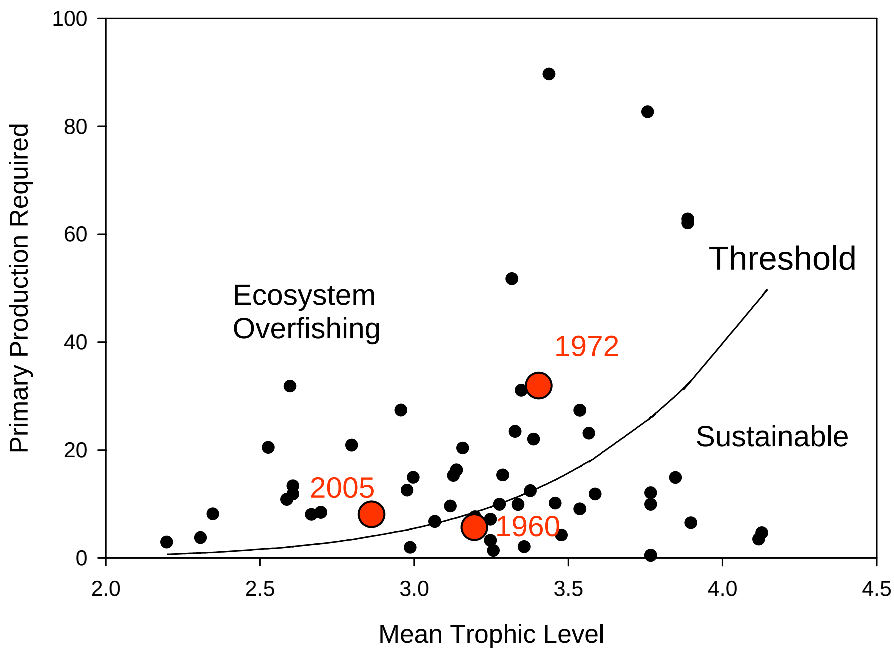

Figure 6. Relationship between mean trophic level and primary production required for observed landings in ecosystems summarized by Tudela et al. (2005) with estimated demarcation point between sustainably fished and overfished systems. Three observations from the Northeast Continental Shelf are shown from the available time series.